



The Influence of Fire on a Rare Serpentine Plant Assemblage: A Five Year Study of Darlingtonia Fens

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Global diversity in light of climate change: the case of ants

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ABSTRACT

Aim To use a fine-grained global model of ant diversity to identify the limits of our knowledge of diversity in the context of climate change.

Location Global.

Methods We applied generalized linear modelling to a global database of local ant assemblages to predict the species density of ants globally. Predictors evaluated include simple climate variables, combined temperature \times precipitation variables, biogeographic region, elevation, and interactions between select variables. Areas of the planet identified as beyond the reliable prediction ability of the model were those having climatic conditions more extreme than what was represented in the ant database.

Results Temperature was the most important single predictor of ant species density, and a mix of climatic variables, biogeographic region, and interactions between climate and region yielded the best overall model. Broadly, geographic patterns of ant diversity match those of other taxa, with high species density in the wet tropics and in some, but not all, parts of the dry tropics. Uncertainty in model predictions appears to derive from the low amount of standardized sampling of ants in Asia, Africa, and in the most extreme (e.g. hottest) climates. Model residuals increase as a function of temperature. This suggests that our understanding of the drivers of ant diversity at high temperatures is incomplete, especially in hot and arid climates. In other words, our ignorance of how ant diversity relates to environment is greatest in those regions where most species occur—hot climates, both wet and dry.

65 **Main conclusions** Our results have two important implications. First, temperature is necessary,
66 but not sufficient, to explain fully the patterns of ant diversity. Second, our ability to predict ant
67 diversity is weakest exactly where we need to know the most, the warmest regions of a warming
68 world. This includes significant parts of the tropics and some of the most biologically diverse
69 areas in the world.

70 **Keywords**

71 Aridity, biodiversity, biogeography, Formicidae, species richness, temperature

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(A) INTRODUCTION

Most pollinators, predators, disease vectors, and pests are insects (Beattie & Ehrlich, 2010), but our understanding of global patterns of insect diversity is still in its infancy (Diniz-Filho *et al.*, 2010). Scientists have yet to examine diversity patterns for most insect taxa, but have made major progress in mapping a few focal groups at coarse spatial grains (e.g. countries and 10° grid cells, see Foley *et al.*, 2007; Pearson & Cassola, 1992; Guénard *et al.*, 2010; Eggleton *et al.*, 1994; Balian *et al.*, 2008). A next step is to document and model patterns of diversity at finer spatial grains, ones at which ecological and evolutionary processes play out. This will be particularly important for understanding how insect diversity, and the services that insects provide, may respond to anthropogenic pressure and a changing climate (e.g. Fitzpatrick *et al.*, in press). We present here a fine-grained global map for ants, documenting both what we know about global ant diversity and, perhaps more importantly, what we do not know.

For vertebrates, maps of diversity are often created by overlaying species range maps (e.g. Rahbek & Graves, 2001; Jetz & Rahbek, 2001, Young *et al.*, 2004; Orme *et al.*, 2005, 2006; Pimm & Jenkins, 2005; Grenyer *et al.*, 2006; Jenkins & Giri, 2008). However, this method is not yet practical for the vast majority of insects. Relatively few insect taxa have had sufficient sampling to produce valid range maps. Even by conservative tallies, only a small fraction of insects has even been described (Hamilton *et al.*, 2010). An exception would be the butterflies, but even for them, maps exist only for some regions (Hawkins, 2010).

An alternative to the range map approach is to take field plot inventories and correlate these estimates of local diversity with environmental variables estimated for the same locations (e.g. Lobo *et al.*, 2004; Kreft & Jetz, 2007; Beck *et al.*, in press). This statistical modelling

96 approach can be useful, both to understand contemporary diversity patterns (e.g. Dunn *et al.*,
97 2009a) and to predict potential changes in diversity as the environment changes. Additionally,
98 such models can be projected across space and through time (e.g. for current and predicted future
99 climates) to reveal places and environments where our understanding of diversity is limited or
100 where the model performs poorly.

101 A common assumption when using correlative models is that the relationships between
102 environment and diversity operate in a similar manner in different parts of the world. Such an
103 assumption is likely to be violated, but to what extent and in what ways remains largely
104 unexplored for insects. For example, to our knowledge, relatively few quantitative samples of the
105 diversity of ants exist for Africa. Does this restrict our ability to explore climate-diversity
106 relationships for ants, or are climate-diversity relationships in Africa similar enough to those in
107 other parts of the world that we can assume generality? If evolutionary history has shaped the
108 African ant fauna such that ants in Africa respond differently to the environment than do ants in
109 other areas, then a region-specific model might be necessary (Ricklefs, 2007). Similar logic can
110 apply to a changing climate. Do we understand what happens to diversity in the extreme climates
111 of today, some of which may be rare and unexplored, but which climate models predict will
112 expand greatly in the future?

113 We focus on these topics using ants because they are ecologically important,
114 conspicuous, and easily sampled in standardized ways. Just as importantly, they are among the
115 most well-known taxa of terrestrial invertebrates, and so represent one of the best-case scenarios
116 in terms of our knowledge of terrestrial invertebrates. To assess our ability to understand the
117 current and potential future patterns of ant diversity, we constructed global regression models
118 and maps of one measure of local diversity, ant species density (number of species per 10×10

km grid cell). We did this by correlating extensive field data on local ant assemblages with a suite of environmental variables. We then compared the environmental sample space of the model to the current and predicted future distribution of climates, highlighting specific climatic and geographic gaps in our knowledge of global ant diversity. In the spirit of S.W. Boggs (1949), we produce a map of ignorance for ants. Like Boggs, we argue that understanding the limits of our current knowledge, particularly in light of future conditions, will reduce our ignorance in the future. We hope that the gaps in knowledge we identify here will be, as Boggs put it “a needed stimulus to honest thinking and hard work.”

(A) METHODS

(B) *Ant assemblage database*

We compiled sampling data for local ant communities from all continents except Antarctica. We present a brief description of the database here, but details appear elsewhere (Dunn *et al.*, 2007, 2009a). The database includes the majority of studies that used standardized methods to sample ants as of January 2010, including additional studies published since Dunn *et al.* (2009a), for a total of 235 published studies. Some studies included multiple sampling events. Studies used in the current analyses met the following criteria: (1) the ground-foraging ant community was sampled using standard (e.g. pitfalls, Winkler litter samples, baits) though not identical field methods; (2) sampling was not trophically or taxonomically limited (e.g. the study did not focus only on seed-harvesting ants); (3) sampling occurred on continental mainlands or large islands (e.g. Madagascar), but not small oceanic islands; and (4) study sites were undisturbed or minimally disturbed natural habitats. Measures of diversity apply to ground-foraging ants only

and exclude both soil-dwelling and canopy ants missed by the sampling methods considered here (Bestelmeyer *et al.*, 2000; Delabie *et al.*, 2000, Weiser *et al.*, 2010).

We converted sample point data to a gridded map with 10×10 km (100 km^2) cells, matching the resolution of the environmental data used in the model (described below). If two or more sites were less than 10 km apart, we combined those data and assigned a central coordinate and total species richness to the combined sites. Species richness for a set of combined sites was calculated by combining their cumulative species lists. When site-level species lists were unavailable, we used the study only if all sites were within 10 km of one another. The final database had 358 records suitable for analysis (Figure 1). Since we counted the number of species per 100 km^2 grid cell, this measure of diversity is most appropriately termed species density (Simpson, 1964; Gotelli & Colwell, 2001). One might think of it as the species richness of a single grid cell. Analyses were also done for 1 km and 5 km grains and those results and discussion are available online as Supporting Information.

Species diversity estimates can be sensitive to the extent of field sampling, and a weak but statistically significant correlation does exist between the number of samples and species density ($R^2 = 0.053$; $p < 0.001$; one outlier with 20,000 samples excluded). To minimize potential bias due to insufficient sampling while still maintaining the bulk of the data, we excluded records having fewer than 20 total samples (e.g. pitfalls, litter samples, baits at a location). While more advanced selection methods exist for choosing well-sampled sites (see Lobo *et al.*, 2004), current data cannot yet support such methods. We also examined the correlation between the area sampled in the field and species density. However, there was no correlation for the 278 records with information on sample area ($R^2 < 0.01$, $P > 0.4$).

(B) *Environmental correlates*

A suite of climatic variables are known to be correlated with ant diversity (Kaspari *et al.*, 2003, 2004; Sanders *et al.*, 2007; Dunn *et al.*, 2009a, b; Vasconcelos *et al.* 2010; Weiser *et al.*, 2010) and are among the few environmental variables for which there are global, future predictions. As such, they are our main focus. For contemporary climate, we evaluated 12 variables from the WorldClim dataset (Hijmans *et al.*, 2005): mean annual temperature, mean temperatures of the coldest month, coldest quarter, warmest month, and warmest quarter, the annual temperature range, temperature seasonality, mean annual precipitation, mean precipitation of the driest month, driest quarter, wettest month, and wettest quarter.

Previous meta-analyses of both vertebrates and invertebrates have found that variables measuring energy and water availability—and the interaction between them—are strong predictors of species diversity (Hawkins *et al.*, 2003a). We evaluated temperature-precipitation interactions using three variables: (1) a simple interaction term of mean annual temperature multiplied by precipitation; (2) potential evapotranspiration (PET); and (3) an aridity index. The PET and aridity data are from Trabucco and Zomer (2009) who used the WorldClim data plus estimates of solar radiation to model PET, and the aridity index is equal to mean annual precipitation divided by PET. To our knowledge, the recently developed aridity and PET datasets have not previously been used for diversity modelling.

Data on predicted climate in 2050 are from Ramirez and Jarvis (2008) using climate scenario SRES A2a. We chose three climate models (CGCM3.1-T47, BCCR-BCM 2, and GISS-AOM) that represent a range of future predictions, but emphasize that our intent is to illustrate potential futures, not judge one model as better than another. We recognize that other climate

models yield predictions that differ in their specifics, particularly with regard to precipitation, though all such models predict net global warming and warming to some extent in all biomes (IPCC, 2007).

Species density, and its correlation with environmental variables, may vary among geographic regions due to historic reasons such as glaciation or evolutionary history (Gaston, 1996; Chown *et al.*, 2004; Ricklefs *et al.*, 2004; Dunn *et al.*, 2009a, b). We evaluated continent and biogeographic realm (Olson *et al.*, 2001; WWF, 2008), and the interactions between environmental variables and these geographic regions, as potential predictors. Although ant diversity was previously shown to be higher in the southern hemisphere, even after accounting for climate (Dunn *et al.*, 2009a), we used continents and biogeographic realms here to allow for the possibility of regional effects above and beyond those captured simply by hemisphere.

Using data from the Shuttle Radar Topography Mission (Rabus *et al.*, 2003), we evaluated elevation as a potential predictor variable because it might capture additional variation in climate missed by climate models. The interpolation methods used to produce the WorldClim data do consider elevation, but the approach is imperfect (Daly, 2006). However, elevation contributed little explanatory power in the models and was not included in the final analyses.

(B) *Model-fitting and Evaluation*

We used generalized linear modelling in JMP 8.0 (SAS, 2008) using the log-link function and a Poisson distribution with species density as the response variable. There were 17 potential predictor variables (12 climate variables, 3 temperature \times precipitation variables, continent, and biogeographic realm) plus the interactions between geographic region and environmental variables. We compared candidate models using both log-likelihood and Akaike's Information

Criterion with the small sample size correction (AICc) (Burnham & Anderson, 2002). Adjusted R^2 's were calculated from a comparison of model predictions to the sample data. We mapped model predictions globally by applying the models to environmental data layers using ArcGIS 9.3 (ESRI, 2009). Areas with climates beyond the range sampled by the ant assemblage database were excluded from predictions. For models with a climate-geography interaction variable, areas were excluded within each geographic region using the interacting climate variable based only on the ant samples within that region.

(A) RESULTS

(B) *Environmental predictors*

Mean annual temperature accounted for more than a third of the variation in ant species density globally and was the best single predictor (41% decrease in AICc, adjusted $R^2 = 0.36$, Table 1). Addition of the precipitation in the wettest quarter of the year, followed by biogeographic realm, improved the model substantially (56% decrease in AICc, adjusted $R^2 = 0.51$, Table 1). The incorporation of the interaction between precipitation and biogeographic realm also improved the model (66.6% decrease in AICc, adjusted $R^2 = 0.67$, Table 1). Additional variables improved model performance only marginally but complicated model interpretation. Plots of the predicted versus observed species density for each model are in the Supporting Information. Model predictors and rankings for 1km and 5 km grains are presented in the supporting information, but in general, the results were similar to those for 10 km grains.

At very high temperatures, the relationship between species density and temperature is extremely variable. In our limited sampling of the hottest ($> 27^\circ\text{C}$ mean annual temperature) and/or most arid areas (< 500 aridity index), species density varies from 0 to 145 species (Table

S3). In the simplest model, that using mean annual temperature only, the model residuals increase with temperature with the regression line having a slope of ~ 0.2 (Figure 2). Reassuringly, the best-performing model has smaller residuals and less increase in those residuals with temperature (slope = ~ 0.1 , Figure 2). Nevertheless, the residuals still increase with temperature across the temperatures sampled. It is possible that this trend would extend to even warmer climates, beyond those where we currently have data.

(B) *Climatic limits*

Many of the world's biomes are represented by well-described, quantitative samples of ants, but the distribution among biomes is biased (Figure 4). The relatively cold tundra and taiga biomes, the wettest temperate forests, and the hottest subtropical deserts have few or no quantitative samples (Figure 4). To some extent, we knew that these climatic regions were under-represented (Dunn *et al.*, 2007), but we explore them here in more detail, particularly in the context of their present and future distribution.

The non-sampled climates represent $\sim 34\%$ of the planet's land area (dark grey in Figure 5). With no empirical ant data to compare with the model predictions, we have no rigorous way to evaluate predictions for such climates, and so we excluded them from our results. The area occupied by these non-sampled climates, and future no-analogue climates, is expected to expand greatly in the future (red in Figure 5). No-analogue climates are those with a mean annual temperature or precipitation beyond what occurs globally today. Considering the CGCM3.1-T47 climate model as an example, 49% of the planet's land area has, or will have in the future, a climate for which we have insufficient data to model ant diversity. Expansion of these non-sampled climates will be almost entirely within the tropics (Figure 5). That expansion is mostly

due to climates becoming hotter, although some areas also become too dry or too wet to model. Other axes of climate, such as seasonality, will also undoubtedly change. For results using other climate models, see Supporting Information.

(B) *Geographic patterns*

Applying the best-performing model globally indicates that ground-foraging ants follow some broad patterns of diversity described for other taxa, with higher diversity in the tropics and lower diversity at higher latitudes (Figure 6). Areas predicted to have relatively low species density include much of North America, Europe, and temperate Asia. Areas predicted to have notably high species densities include the Amazon, Congolese and West African forests, scattered localities in eastern Africa, and parts of Madagascar, India, and Southeast Asia. However, many of the areas predicted to have high species densities are in climatic regions poorly represented in the sample data (see previous section).

(A) **DISCUSSION**

We find that ant diversity, at least qualitatively, tracks that of other terrestrial plants and animals, with high diversity in the wet tropics and low diversity in the cold and dry subarctic. Importantly, our models highlight what we know in light of climate change, but even more importantly, what we do not know about current or future distributions of ant diversity.

Two climate variables plus an effect of biogeographic realm accounted for most of the variation in ant species density. The correlation with climate is expected, as many previous studies have documented links between climate and diversity both for ants (e.g. Kaspari *et al.*, 2000, 2003; Dunn *et al.*, 2009a; Vasconcelos *et al.*, 2010) and other taxa (e.g. Hawkins *et al.*,

2003a; Kreft & Jetz, 2007). The importance of biogeographic realm in the models, particularly the interaction between biogeographic realm and precipitation, suggests that climate-diversity relationships for ants vary by region. Even though biogeographic divisions have been derived largely using plants and vertebrates, it appears that they still help explain diversity patterns for ants. In line with previous work (Dunn *et al.*, 2009a), the biogeographic regions in the southern hemisphere tended to be more diverse. Just as for other taxa such as birds (Hawkins *et al.*, 2003b), global models to explain ant diversity need to account explicitly for geography, and by extension evolutionary history, not just the current local environment. This task becomes more difficult as one considers not just the present but also the future.

Our primary focus though was not the specific correlates of diversity, but rather the limits posed when predicting diversity of ants both geographically and across time. Our results highlight specific climates (Figure 4) and geographic areas (Figure 5) that myrmecologists have yet to sample systematically for ants. These regions tend to be extreme climates (very hot or cold, very wet or dry), where ants might not always be diverse, but may still be very important from the perspective of their ecological roles (Wardle *et al.*, in press).

The climates predicted to expand most though, under the climate models considered here, are the hot climates, both wet and dry. The fact that temperature is positively correlated with ant species density naively suggests that as hot places get hotter, species density should increase. Global models though can hide locally important phenomena. For one, species do not track climate perfectly, particularly among biogeographic regions. Even if there are many species that could live in a climate, they might not be able to colonize the regions with that climate. Just as significantly in hot regions, factors other than temperature alone limit diversity. Some of the hottest places on the planet, such as the Sahara, actually have very low ant diversity. It is at this

high end of the temperature gradient, where diversity can be extremely high or extremely low, that we reach the limits of our current knowledge. Simply put, we do not yet know enough about ants in extremely hot climates around the world to understand fully the impact of further warming on these under-explored assemblages.

We see three challenges to improving the ability to understand diversity in the hot, expanding climates. First, as we have mentioned, the hottest conditions are poorly sampled, likely contributing to the uncertainty of model predictions within these climates. We need systematic samples of ants in hot climates of all types. Moreover, because climate-diversity relationships vary among biogeographic regions, we need samples from similar climates in all biogeographic regions. Second, the influence of precipitation appears to differ among regions and is dependent on temperature, resulting in complex effects that are difficult to capture in a global model. A few previous studies of ant diversity have suggested that precipitation is more influential at high temperatures than at low temperatures (Marsh, 1986; Heatwole, 1996; Pfeiffer *et al.*, 2003). The handful of studies from the very hottest studied ant communities (Table S3), do suggest a tendency for drier places to have fewer species (top of Table S3), whereas warm but slightly wetter areas tend to have many more species (bottom of Table S3). Further discussion of some of the best studies of ants in the hottest and most arid parts of the world is available in the online Supporting Information. These studies lead us to conclude that the relationship between precipitation and diversity in the hottest regions needs more study, as do the traits of species in such regions not just to deal with heat, but also to deal with desiccation.

A third challenge when considering ants in a warmer world is that regions may differ in the extent to which their species are able to adapt to hotter conditions (Morton & Davidson, 1988; Morton & James, 1988; Andersen, 1997). If climatic niches are more conserved in some

lineages than in others (Machac *et al.*, in press), those lineages might more often fail to evolve the traits necessary to adapt to drastic climate changes than would species in lineages with more evolutionarily labile climatic niches (Wiens *et al.*, 2006, 2010; Algar *et al.*, 2009). In other words, faunas in some warm areas may be intrinsically better able to adapt evolutionarily to further warming of their climate than are faunas in other areas. Whether such biogeographic differences in adaptability exist, due to history or lineage effects, is important. It could mean that particular faunas may be disproportionately likely to thrive in a warmer future, possibly contributing invasive and introduced species.

Even more difficult than modelling ant diversity in expanding climates will be trying to understand the fate of places predicted to have no-analogue climates. These will tend to be hotter than any existing climates, as was shown in the context of a traditional Whittaker biome plot (Figure 4). While our model suggests that ever warmer sites will tend to have ever more species, as we have discussed the uncertainty increases at higher temperatures. As well, an aridity threshold appears to exist beyond which species density sharply decreases. The known hot and extremely arid sites actually have very few or even just one or two species (Table S3), although studies from such conditions are too few to have much influence in models. We also emphasize that our definition of no-analogue here is a conservative one. Climates may also be no-analogue for variables not in the model, such as the variability of precipitation and temperature (e.g. Williams *et al.*, 2007).

In brief, warmer tends to mean more species, but not always, and in those places most similar to the expanding climates of the future, models perform the worst. This poorer performance may relate to the way that precipitation influences diversity at higher temperatures,

but as yet our global sampling of ant diversity in the warm climates is insufficient to model the relationship confidently.

Our results provide a measure of what we do and do not know. They also provide a road map for future research. The hottest regions mapped in Figure 3 have conditions most like those that will be expanding around us, and so they may prove disproportionately interesting for future study. Having good samples from these regions, and studies of the physiological tolerances of species in them, could tell us much about the future shape of regional ant faunas. Some of these areas have been studied, just not from an ecological perspective. Records of individual species exist, such as in systematic revisions, but there is no information on their abundance, life histories, or ecology, largely because almost no one goes to do community ecology in places where there is not a community to study, or a sparse one. Many of these areas are also physically harsh, making for exceptionally difficult fieldwork. However, verifying that an area has few or no species, and knowing why, is valuable information, particularly as the geographic coverage of such conditions grows.

The future expansion of today's extreme environments, and the likely emergence of no-analogue climates, is new territory for biodiversity (Williams *et al.*, 2007; Fitzpatrick & Hargrove, 2009). Where and how fast these climates develop will likely have major implications for animal and plant life (Loarie *et al.*, 2009). The limits of our current knowledge of ants coincide with these expanding climates of the future. The best strategy is perhaps to focus more of our efforts in the climates similar to those predicted to expand in the future, even if they are uncomfortable to visit, as they will expand whether we study them or not.

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552 **Supporting Information**

553 Additional Supporting Information may be found in the online version of this article:

554 **Appendix S1** Methods and results for the 1 km and 5 km grains of analysis.

555 **Appendix S2** Discussion of existing studies about ants in extremely hot and arid places.

556 **Figure S1** Distribution of survey locations in the ant assemblage database for the 1 km and 5 km
557 grains of analysis.

558 **Figure S2** Species density of ants predicted at the 1 km and 5 km grains using the best-
559 performing model.

560 **Figure S3** Plots of predicted versus observed species density for each of the 10 km grain models.

561 **Figure S4** Distribution of climates that have not been adequately sampled for ants, shown under
562 contemporary climate and the expansion of the non-sampled and no-analogue climates projected
563 for 2050 for two climate.

564 **Table S1** Models of global species density of ants at 1 km and 5 km grains.

565 **Table S2** Pearson correlations between predictions of species density at different grains.

566 **Table S3** Attributes of sampled hot and arid sites.

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573 **(A) BIOSKETCHES**

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575 research program focuses on biodiversity and its conservation, with a focus on Brazil, the
576 western Amazon, and assessment of the global protected area system.

577 Author contributions: C.N.J., R.R.D., M.D.W., N.J.S., M.C.F. developed the concepts and
578 structure of the article. C.N.J. designed and produced the figures. Members of the global ant
579 coalition (<http://www.antmacroecology.org>) collected the data and are broadly interested in
580 understanding ant diversity and conservation. All authors contributed to writing of the article.

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582

583 **Figures and Table Legends**

584 **Figure 1** Map of standardized survey locations included in the ant assemblage database, both
585 those used in the 10 km grain analyses (filled circles) and those excluded as unsuitable for our
586 analyses (open circles). Map uses an equal area projection.

587 **Figure 2** Plots of the absolute values of model deviance residuals versus mean annual
588 temperature. Lines are simple linear regressions. Model residuals tend to increase with mean
589 annual temperature, suggesting a decline in model performance with rising temperature. The
590 decline is most pronounced in the simplest model using only temperature (A). The best-
591 performing model (B) has generally smaller residuals and a slower increase in those residuals
592 with temperature, as indicated by a lower slope of the regression line. One point with a residual
593 of 27.8 is not shown in the temperature only model (A).

594 **Figure 3** Map of areas of extreme aridity (< 500 on aridity index, Trabucco & Zomer 2009) and
595 areas that are extremely hot (> 27°C mean annual temperature) but not necessarily arid. Points
596 marked on the map indicate all sites in the ant assemblage database that are in arid and/or hot
597 areas, including those used for modelling (black dots) and those that did not meet our criteria for
598 use in modelling (blue dots).

599 **Figure 4** Classic Whittaker plot (Whittaker, 1975) of biomes. Sites from the ant assemblage
600 database are plotted at their corresponding temperature / precipitation coordinate, showing the
601 uneven sampling of the climate space. Very dry and very hot climates have particularly sparse
602 sampling. Climates predicted to occur in the future (2050) but beyond current biomes appear in
603 grey.

Figure 5 Distribution of climates that have not been adequately sampled for ants, shown under contemporary climate (dark grey, 34% of land area) and the expansion of these non-sampled climates, plus the emergence of no-analogue climates, projected for 2050 (red, 15% of land area). Together these areas cover 49% of the planet's surface and are indicative of our ignorance of the future world. Map uses an equal area projection.

Figure 6 Species density of ants predicted at a 10 km grain using the best-performing model, which includes: mean annual temperature, precipitation in the wettest quarter of the year, biogeographic realm, and the interaction between precipitation and realm (see Table 1 for details of all models). Dark grey areas are non-sampled climates as described in figure 5. Map uses an equal area projection.

Table 1 General linear models of global species density of ants at a 10 km grain. The percent change for Δ AICc represents the percent decline in the AICc value relative to that of the intercept only model. MAT = mean annual temperature, Precip = precipitation in the wettest quarter of the year, Realm = biogeographic realm.

Table 1

Variables	R² ^a	AICc	Δ AICc (-%)	Δ Log likelihood	DF
MAT + Precip + Realm + Precip*Realm	0.67	5472	-10901 (66.6%)	5463	12
MAT + Precip + Realm	0.51	7205	-9168 (56.0%)	4591	7
MAT + Precip	0.37	9383	-6990 (42.7%)	3497	2
MAT	0.36	9663	-6710 (41.0%)	3356	1
Intercept only	-	16373	-	-	0

^a For GLZ models this is sometimes referred to as a pseudo R².

Figure 1

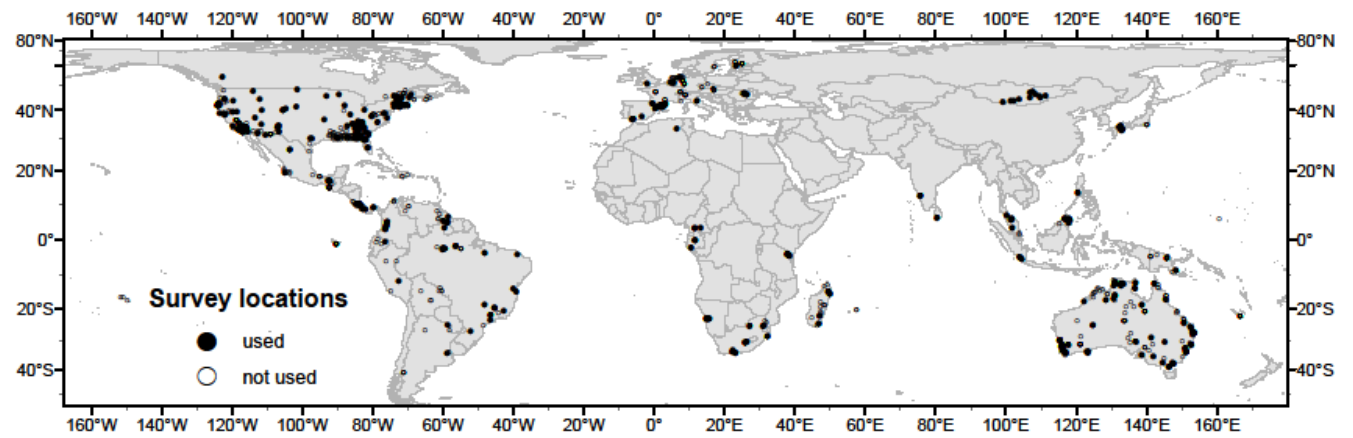


Figure 2

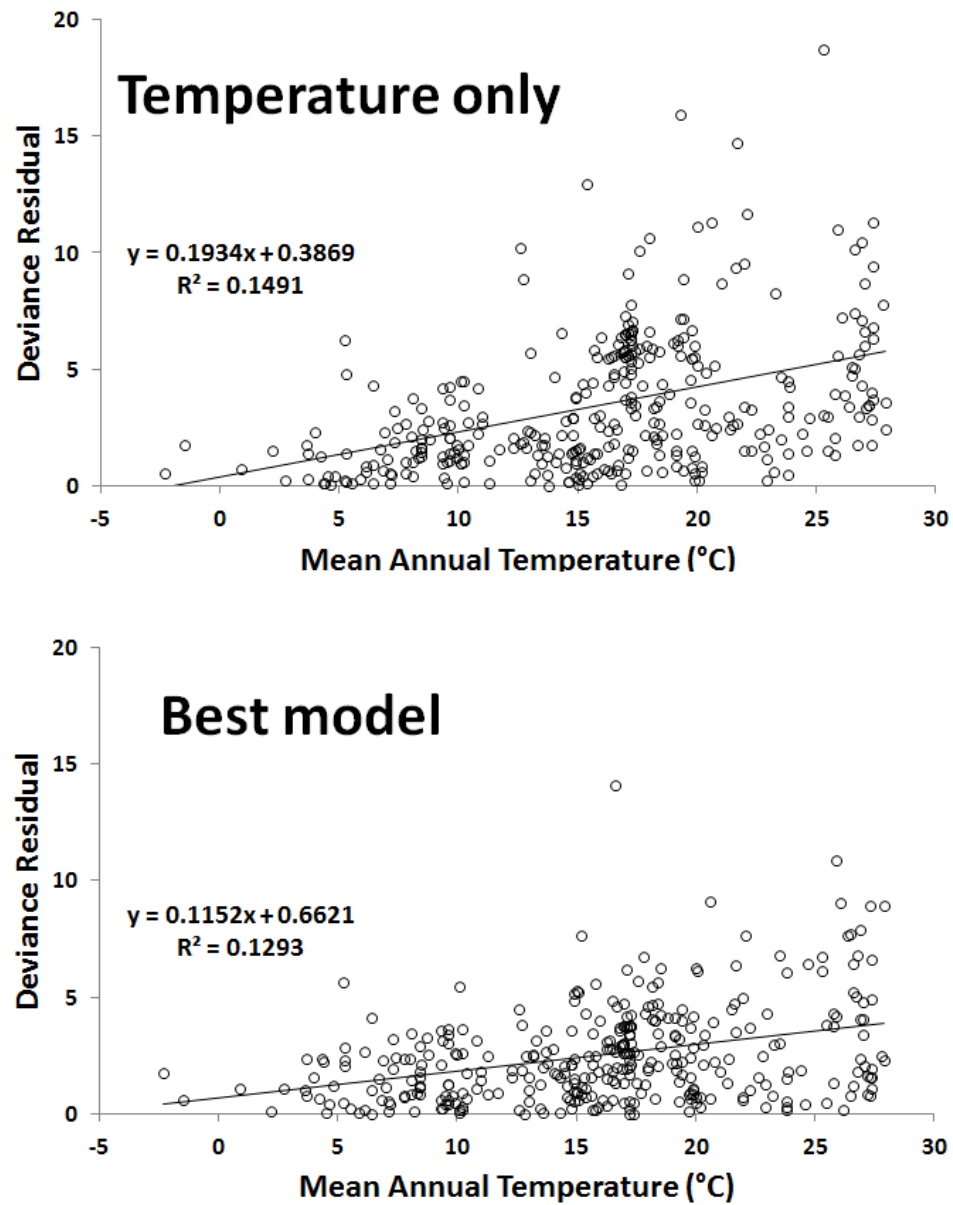


Figure 3

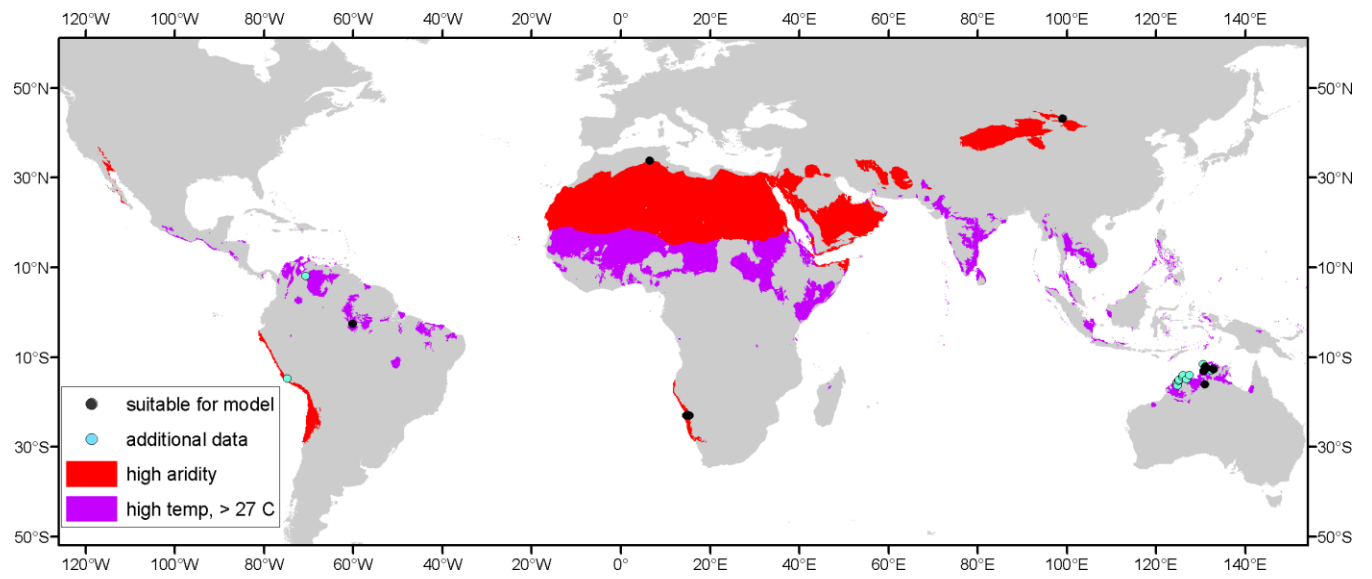


Figure 4

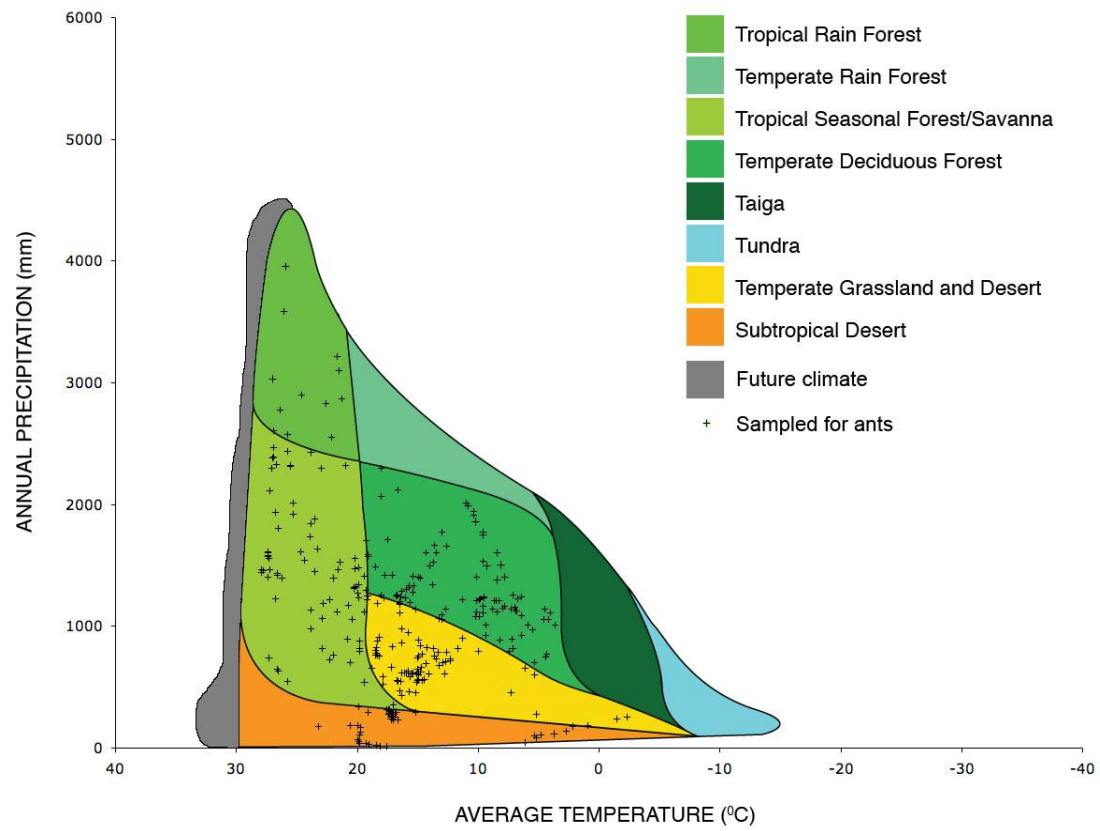


Figure 5

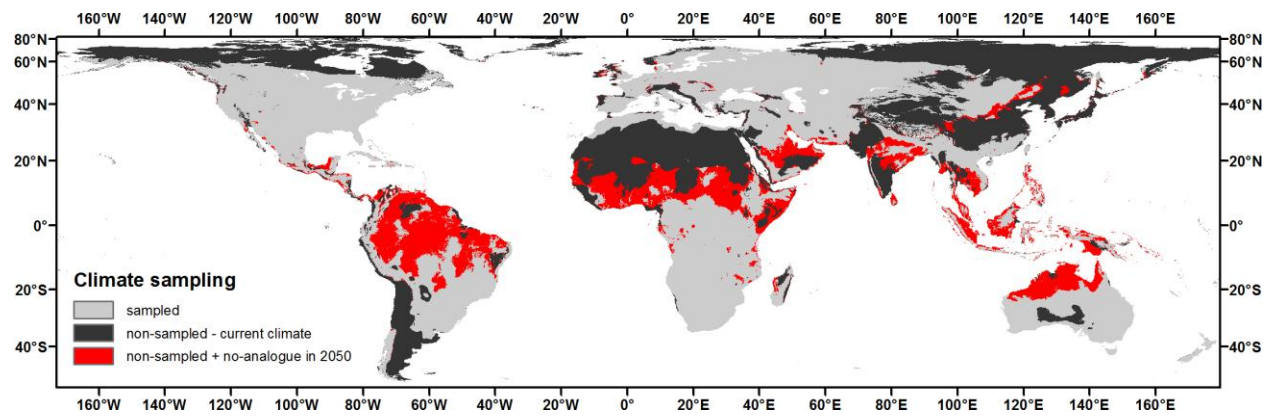
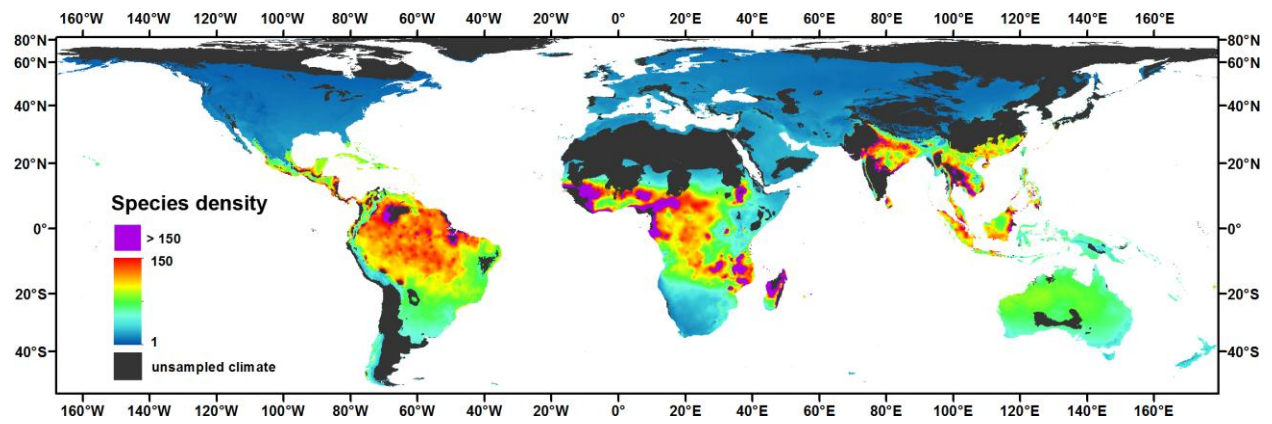


Figure 6



SUPPORTING INFORMATION

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Appendix S1 Methods and results for the 1 km and 5 km grains of analysis.

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Figure S1 Distribution of survey locations in the ant assemblage database for the 1 km and 5 km grains of analysis.

Figure S2 Species density of ants predicted at the 1 km and 5 km grains using the best-performing model.

Figure S3 Plots of predicted versus observed species density for each of the 10 km grain models. Lines have a slope of one, indicating a perfect correspondence. MAT = mean annual temperature, Precip = precipitation in the wettest quarter of the year, Realm = biogeographic realm.

Figure S4 Distribution of climates that have not been adequately sampled for ants, shown under contemporary climate and the expansion of the non-sampled and no-analogue climates projected for 2050 for two climate models (GISS-AOM and BCCR-BCM2) using greenhouse gas emissions scenario A2a.

Table S1 Models of global species density of ants at 1 km and 5 km grains.

Table S2 Pearson correlations between predictions of species density at different grains.

Table S3 Attributes of sampled hot and arid sites. A subset of these sites that have precise geographic coordinates appears in Figure 3.

Appendix S1

Effects of spatial grain size

To explore the possible effects of spatial grain size (i.e. the size of grid cells for the analysis) on our ability to model environment-diversity relationships, we analysed the data at three different grains (grid cells of 1, 5, and 10 km on a side). Methods for calculating species density at the 1 km and 5 km grains were identical to those described in the main text for the 10 km grain, but adjusted for the smaller grid cell size. The final database had 204, 305, and 358 records suitable for analyses at 1 km, 5 km, and 10 km grains respectively (locations shown in Figures 1 and S1). Fewer records were suitable for finer grained analyses, primarily because the geographic coordinates for many studies had insufficient precision.

The model selection results were similar for all three grains of analysis. Model rankings were identical, with models retaining their broad pattern of improvement as variables were added (Tables 1 and S1). There was a general decline in R^2 from finer to coarser grains (Tables 1 and S1). We suspect this was due to the wider geographic and climate coverage included at coarser grains, and so there was more variability in the data for the model to explain. Another possibility is the increasing difference between the scale of actual field collections and the grain of the analysis. These explanations are speculative though.

Predictions of species density globally for different grains were similar (Figures 6 and S2) with Pearson correlations between the predictions of species density at different grains all above 0.71 (Table S2). The most noticeable differences are between the 1 km grain predictions and those of coarser grains, where the 1 km model predicted Africa to have generally higher species density and the Neotropics lower species density. However, it is at the 1 km grain that

there are the fewest suitable records upon which to base a model, with substantially fewer records available for Asia, Africa, and South America compared to the 5 km and 10 km grains (Figures 1 and S1). Consequently, more of the world is also excluded from modelling at the 1 km grain because the smaller dataset samples less of the world's climates (e.g. much of Asia, Australia, the Middle East, and Africa were excluded).

From our analyses, we could not confidently discern effects due specifically to the grain of analysis. We found most studies to be suitable for use at a 10 km grain. Some studies did not include precise enough locality data to use them at a 5 km grain, but most did. For the 1 km grain, 43% of the records were unsuitable for our analyses, including most of the studies in Africa, Asia, and South America.

Appendix S2

Ants in hot and arid places

While across much of the range of conditions experienced by ants the patterns of diversity seem relatively simple, this is far from the case in hot and arid sites. Even a statement as simple as “drier conditions decrease diversity when precipitation is low” is difficult to make without qualifiers. For example, the exceptionally high ant diversity of arid Australia is maintained to at least 200 mm/year of rainfall (Greenslade, 1978; Hoffmann & James in press), with communities dominated numerically and ecologically by species of *Iridomyrmex*, and species of *Melophorus*, *Monomorium*, *Camponotus* and *Rhytidoponera* are highly abundant (Andersen, 2003). In contrast, the Tabernas desert and Cabo de Gata area of southeastern Spain are similarly dry with

230 mm and 150 mm/year of rainfall respectively, but tend to be species poor with from 4 to 11 species per plot (X. Cerdá & R. Boulay, unpublished data) and a total regional richness of just 25 species (Tinaut *et al.*, 2009), far fewer than similarly dry parts of Australia. The most abundant species in these Spanish sites are *Lepisiota* (formerly *Acantholepis*) *frauenfeldi*, *Monomorium subopacum*, *Tapinoma nigerrimum* and the thermophilous *Cataglyphis iberica*. Even the somewhat wetter Mediterranean habitats (forests, grasslands, shrublands) of the region tend to be relatively poor with between 11 and 15 species (Retana & Cerdá, 2000).

The ant fauna is also relatively depauperate in arid parts of Africa, as in Spain, although the composition of the fauna is different. In the pre-Saharan steppes (120 mm/year) and Saharan desert (32 – 150 mm/year), the thermophilic genus *Cataglyphis* is common, just as in Spain, but there is a greater diversity of the granivorous *Messor* (Marsh, 1986) and *Lepisiota frauenfeldi* and *Camponotus thoracicus* are locally abundant (Bernard, 1958; Délye, 1968; Heatwole & Muir, 1991). Elsewhere in Africa, species richness tends to decline as rainfall decreases and is generally low in arid climates. In the dune fields and gravel plains of Namibia (~100 mm/year of rainfall), only 36 species were found in an area of approximately 60 km² (Marsh, 1986). In Northern Sinai in Egypt (<100 mm/year), local richness ranges from zero to 11 species with a total of 27 species for all of Egypt (El-Moursy *et al.*, 2001). Comparatively higher richness has been recorded on the Arabian Peninsula, although this may be due to higher rainfall and greater vegetation cover in some areas (Collingwood, 1985; Collingwood & Agosti, 1996). Other surveys in southern Africa find from 9 species in semi-arid areas (300-350 mm/year) to a mean of 5.5 species in drier areas (<150 mm/year) (Koch & Vohland, 2004). The subfamily Myrmicinae tends to dominate, particularly granivorous species of *Tetramorium* and *Monomorium*. Highly thermophilic *Ocymyrmex* species are also a conspicuous addition.

The lower richness in African and European arid areas compared with Australia is possibly due to two factors. First, the average rainfall is simply much lower in parts of Africa than in the Australian arid zone, with large areas receiving 100 mm/year of rainfall or less. Australia has no such areas of extreme aridity (<100 mm/year). Second, in the most arid parts of Africa the vegetation cover, which provides a more varied microclimate, a range of nesting sites, as well as an important source of carbohydrates, is also lower than in Australia.

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Table S1 General linear models of global species density of ants at 1 km and 5 km grains. The percent change for Δ AICc represents the percent decline in the AICc value relative to that of the intercept only model. MAT = mean annual temperature, Precip = precipitation in the wettest quarter of the year, Realm = biogeographic realm.

1 km

Model	R^2 ^a	AICc	Δ AICc (-%)	Δ Log	
				likelihood	DF
MAT + Precip + Realm + Precip*Realm	0.83	2425	-5448 (69.2%)	2737	12
MAT + Precip + Realm	0.78	2612	-5261 (66.8%)	2638	7
MAT + Precip	0.42	3867	-4006 (50.9%)	2005	2
MAT	0.43	3907	-3966 (50.4%)	1984	1
Intercept only	-	7873	-	-	0

5 km

Model	R^2 ^a	AICc	Δ AICc (-%)	Δ Log	
				likelihood	DF
MAT + Precip + Realm + Precip*Realm	0.74	3973	-7839 (66.4%)	3932	12
MAT + Precip + Realm	0.45	5588	-6224 (52.7%)	3119	7
MAT + Precip	0.31	7223	-4589 (38.9%)	2297	2
MAT	0.31	7310	-4502 (38.1%)	2252	1
Intercept only	-	11812	-	-	0

Table S2 Pearson correlations between predictions of species density at different grains.

Predictions were restricted to those areas that were predictable at all grains.

Comparison	Correlation
1 km x 5 km	0.713
1 km x 10 km	0.730
5 km x 10 km	0.928

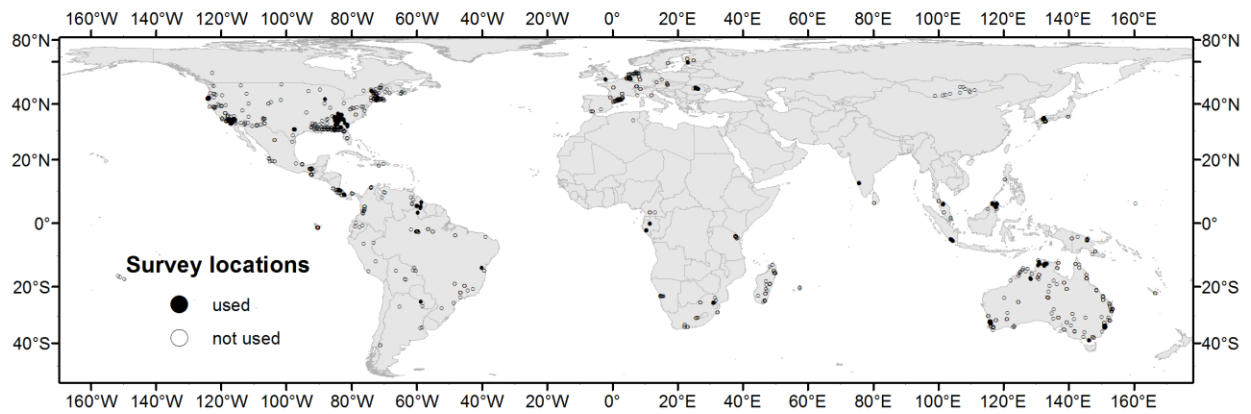
Table S3 Attributes of sites indicated in Figure 3. “Arid” indicates that the locality had an aridity index value <500. “Hot” indicates that the locality had a mean annual temperature >27°C, but was not arid. While the most arid sites sampled tend to have very few species, the hottest non-arid sites were consistently diverse, even though these sites included conditions close to the highest temperatures experience on terrestrial Earth. Sampling types used in the study are coded as: P = pitfalls; B = baits; L = litter; S = soil; H = hand collecting.

[illegible]

Hot	74	Australia	Australia	27.4	1924	PB	Andersen & Patel 1994
Hot	47	Australia	Australia	27.4	60	PL	Andersen & Reichel 1994
Hot	43	Australia	Australia	27.8	45	P	Andersen & Sparling 1997
Hot	81	Australia	Australia	27.9	118	P	Andersen 1991
Hot	145	Australia	Australia	27.9	1280	PB	Andersen 1992
Hot	145	Australia	Australia	27.1	448	P	Andersen <i>et al.</i> 2004
Hot	74	Australia	Australia	27.2	640	PL	Andersen <i>et al.</i> 2006
Hot	19-41	Australia	Australia	27.3-28.1	45	PBLH	Andersen & Majer 1991
Hot	16	Australia	Australia	27.4	60	B	Clay & Andersen 1996
Hot	14 - 38	Australia	Australia	27.7	20	PB	Greenslade 1985
Hot	70	Australia	Australia	27.3	300	P	Hoffmann 2000
Hot	91	Australia	Australia	27.3	480	P	Hoffmann 2003
Hot	140	Australia	Australia	27.3	240	PLSH	Hoffmann <i>et al.</i> 1999
Hot	28-51	Australia	Australia	27.4	30-90	PH	Reichel & Andersen 1996
Hot	143	Brazil	S. America	27.1	360	L	Vasconcelos <i>et al.</i> 2000
Hot	32	Venezuela	S. America	27.4	1	L	Ward 2000

Figure S1 Distribution of survey locations in the ant assemblage database for the 1 km and 5 km grains of analysis. Those suitable for analyses at a particular grain are marked with black circles while those excluded as unsuitable are marked with open circles. Maps use an equal area projection.

1 km



5 km

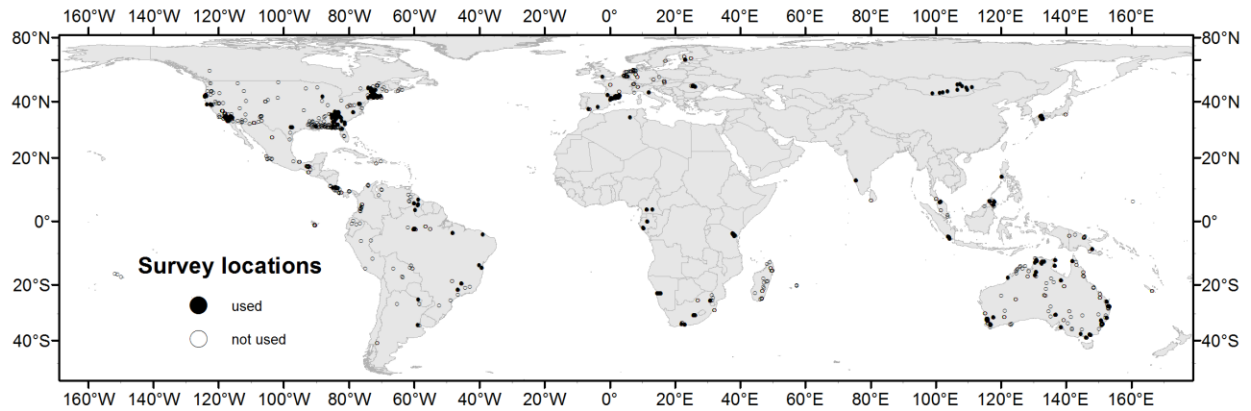
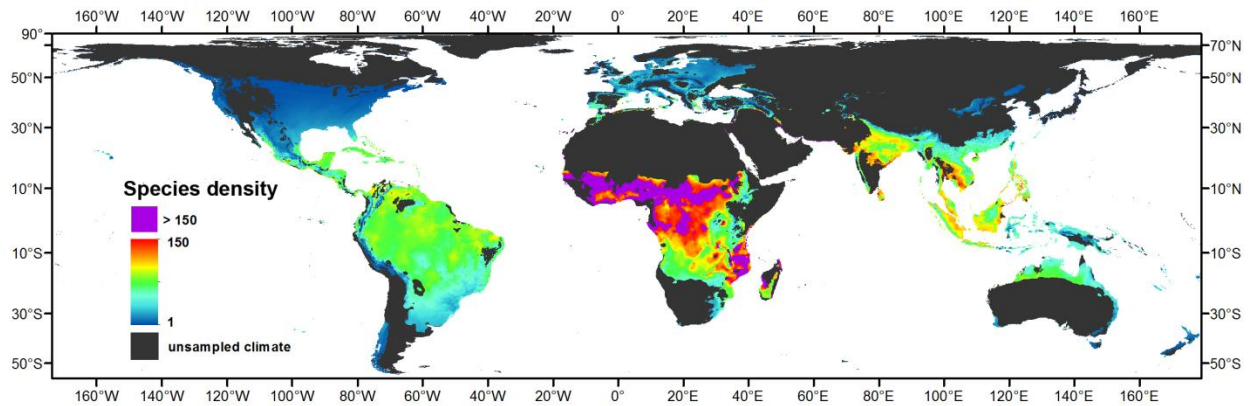


Figure S2 Species density of ants predicted at the 1 km and 5 km grains using the best-performing model, which includes: mean annual temperature, precipitation in the wettest quarter of the year, biogeographic realm, and the interaction between precipitation and realm (see Table S1). Dark grey areas are non-sampled climates as described in figure 5. Maps use an equal area projection.

1-km



5-km

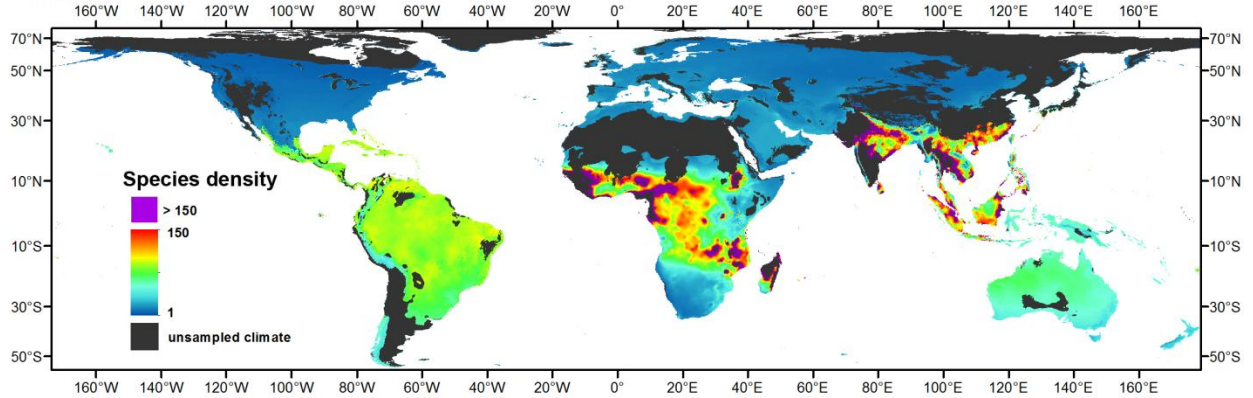


Figure S3 Plots of predicted versus observed species density for each of the 10 km grain models.

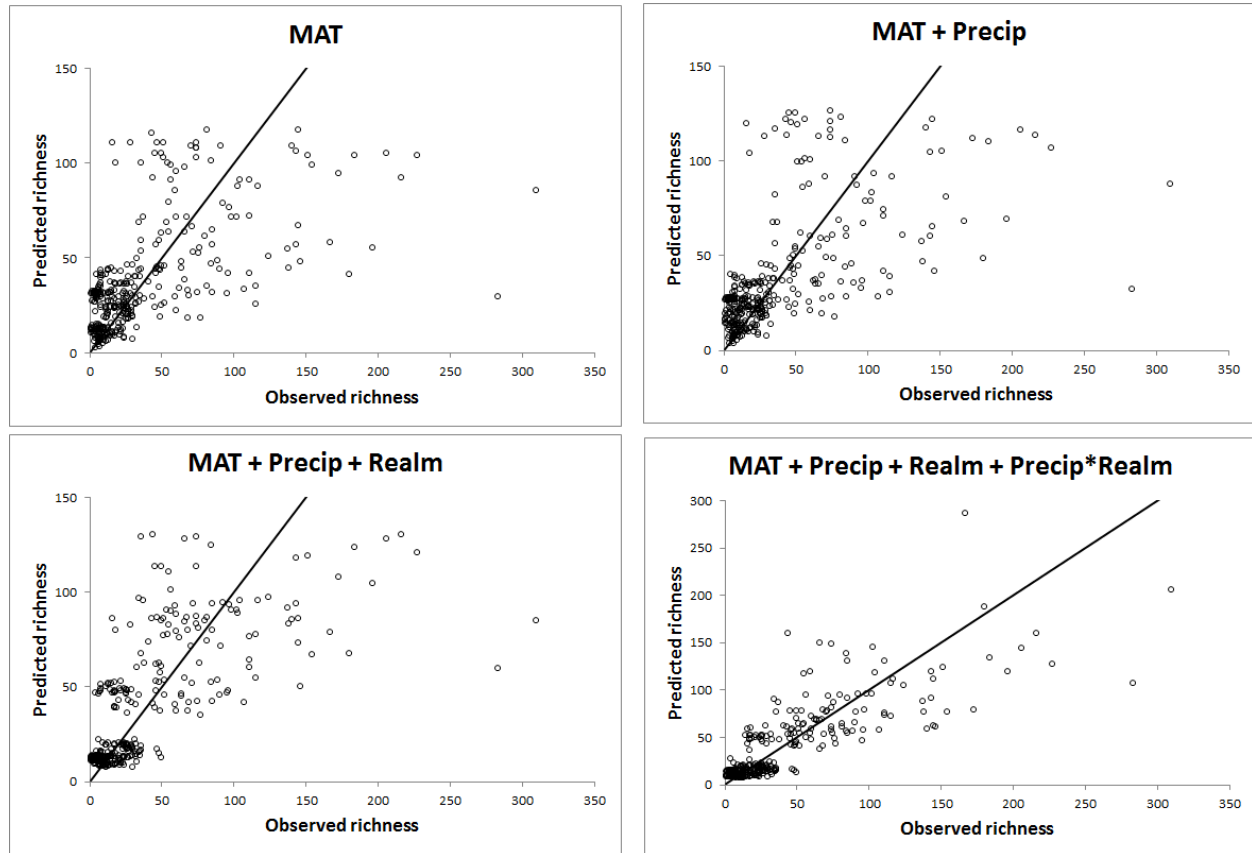
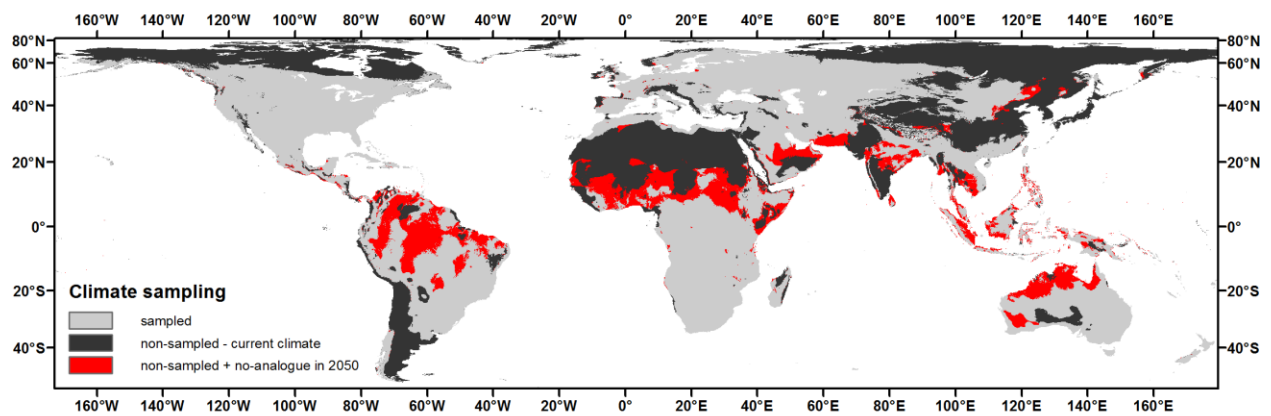


Figure S4 Distribution of climates that have not been adequately sampled for ants, shown under contemporary climate (dark grey, 34% of land area) and the expansion of these non-sampled climates, plus the emergence of no-analogue climates, projected for 2050 (red) for two additional climate models (GISS-AOM and BCCR-BCM2) using climate emissions scenario A2a. Together these areas are indicative of our ignorance of the potential future world. Maps use an equal area projection.

GISS-AOM



BCCR-BCM2

